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EGGS AND LARVAE SURVEY
WITH EMPHASIS ON EARLY
LIFE HISTORY OF MARINE
FISH RESOURCES

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## FOREWORD

One of the current concerns of fisheries biology is to clarify the reason for annual fluctuations in fish populations. The ability of a population to replace itself is determined by the age structure, growth and fecundity of the mature stock. The high fecundity of many marine fishes implies that an extremely high rate of mortality must be experienced by each year class. Most of this mortality occurs during the pelagic larval stage, and for this reason the characteristics of larval mortality are closely related to the basic problems in the population dynamics of fishes.

This paper has been prepared with the intention of summarizing the existing knowledge about the eggs and larvae and the early life history of marine fishes. It is based on revisions and summeries of several lectures presented by the author at regional training courses on fishery stock assessment and fishery statistics held at SEAFDEC, Bangkok, in September - October, 1981.

It is the author's hope that the present paper will be of value to SEAFDEC trainees as one of the first steps towards understanding the problems of fisheries biology.

## 1. BACKGROUND KNOWLEDGE ABOUT FISH POPULATION

### 1.1 Life history

The term "life history" is often used to denote the whole life of fish population and can be regarded as the life cycle with a circulating system (Fig. 1).


Fig. 1 Life cycle of fish population

However, no discriminative system of developmental stages such as shown in Fig. 1, has been universally adopted to cover all fish populations, other systems have been proposed by fisheries biologists (Table l) reflecting the slight differential forms existing among fish species.

Table 1. Discrimination of developmental stages


The fish populations which come into the fishing ground in young, immature and adult stages can be harvested (utilized) by fisheries. In the terminology of fisheries biology, this is known as "recruitment". The fact that the amount of biomass of recruitment would be determined by the amount of biomass of early life stage of a fish population is self-evident. There seems to be a rule that the numerical value of a year class is apparently stated at a very early age which has been pointed out as a "critical period" by Hjort (1914). Thus the important factors which control the density or abundance of a fish stock must be wholly contained within the early life stages. (Fig. 2) This is the reason why further studies on early life history are required. Although the "critical period" hypothesis of the cause of fluctuations in the year-class sizes of marine fish was postulated nearly seventy years ago, little evidence with which to test the hypothesis has been accumulated since then. This is owing mainly to low precision of field data, accompanied by sampling errors (physical and biological errors) but also owing to the lack of knowledge about the early life history of marine fishes. Study of early life history has a world-wide significance from the standpoint of development of stock assessment studies.


Fig. 2 Schematic representation of theoretical
types of survival curve
1.2 Early life history

### 1.2.1 Characteristics of eggs

Marine fishes inhabiting the epipelagic layer of both coastal and open waters of ocean are called pelagic fishes. On the other hand, the fishes whose main habitat is around the bottom zone of the sea are called demersal fishes.
Table 2. Fecundity and characteristics of spawning of marine fish species


The characteristics of spawning are different for pelagic and demersal fishes (Table 2). The eggs of marine fishes are roughly classified into two types; epipelagic and demersal. Demersal eggs are further classified into non-adhesive, adhesive and entwined eggs. The majority of pelagic fishes such as sardines, mackerels, scads, tunas and marlins which inhabit the epipelagic layer both of coastal and open waters of the ocean lay epipelagic eggs but some particular fishes such as sauries and flying fishes have entwined demersal eggs. On the other hand, the majority of demersal fishes usually have demersal eggs. As a rule, pelagic fishes of the open sea tend to have a greater number of eggs than demersal fishes, and the amount of spawned eggs (fecundity) increases with the increase in body size of the mother fish.

### 1.2.2 Stock-recruitment relationship

For most species of marine fish, the number of eggs per female (E) increases sharply with the body length ( $L$ ) or age of the mother; this can be formulated as :

$$
\begin{align*}
E= & a L+b \text { or } E=a L^{b}  \tag{1}\\
& (a \text { and } b \text { are constants) }
\end{align*}
$$

In the open sea, the eggs and larvae are transported far away from the spawning ground by the ocean currents and as a result, the majority of spawned eggs perish before hatching or soon after because of unfavorable food conditions. Thus it could be expected that a vastly multiparous production of eggs in the case of pelagic fishes must be an adaptive strategy necessary for the survival of species.

Fecundity of prolificacy of marine fishes can be estimated by the gravimetric, volumetric and Reibisch's methods, and further analyses are possible by using the following formula:

$$
\begin{equation*}
\mathrm{R}=\mathrm{E} \cdot \oint \cdot \Psi \tag{2}
\end{equation*}
$$

where, $\oint$ and $\Psi$ are the hatching rate of eggs and the survival rate of larvae respectively, and $R$ is the recruitment.

The stock-recruitment relationship can be expressed by either of the following formulas for the Ricker type and the Beverton and Holt type reproduction curves, depending on the type of density-dependent mortality:

$$
\begin{align*}
& R=a E e^{-b E} \quad \text { (Ricker type) }  \tag{3}\\
& R=\frac{a}{b+1 / E} \quad \text { (Beverton \& Holt type) } \tag{4}
\end{align*}
$$

When a significant linear relationship between $E$ and $l_{n} R / E$ is obtained in Formula (3), the application of this curve is useful:

$$
\begin{equation*}
l_{n} R / E=l_{n} a-b E \tag{5}
\end{equation*}
$$

Similarly, Formula (4) can be translated into:

$$
\begin{equation*}
E / R=1 / a+(b / a) E \tag{6}
\end{equation*}
$$

Thus, we cant get $a$ and $b$ values under the application of linear regression lines of $l_{n} R / E$ on $E$ and $E / R$ on $E$.

These stock-recruitment relationships reveal the fact that a fish population, even when not exploited, is limited in size; that is, it is held at some more or less fluctuating level by natural controls and these natural controls act strongly in the early stages of the life history.
2. FIELD SURVEYS AND REARING EXPERIMENTS ON EARLY LIFE HISTORY
2.1 Egg and larval stage

### 2.1.1 Ecological value of egg size

It is considered that the biological value of the size of the egg would best be indicated by the percentage survival of the offspring in the sea, but very little evidence with which to test this assumption has been accumulated.

Hempel (1965) conducted rearing experiments on larval survival of two unit stocks of European herring and confirmed that the large-sized eggs contained more yolk than the small-sized eggs and that larvae with plentiful yolk reserves could endure starvation longer than the ones with small sacs (Fig. 3).


FIGURE 3. Different development of larvae of summer and winter spawners, due to difference in egg size. Development in days at $8^{\circ} \mathrm{C}$. Larvae not fed. p.n.r. = point-of-no return. The vertical bars indicate the dry weight of a) yolk and chorion at fertilization, b) of yolk and larval body at hatching and c) of the larval body at the end of the yolk sac stage.

The figures refer to the duration of incubation, yolk sac stage and starvation period (after resorption of the yolk). (After Hempel, 1965)

The point-of-no-return (PNR) in this figure means the point (critical period) at which survival is impossible even though sufficient food is supplied. Studies on the point-of-no-return have been carried out by many scientists (Lasker et al. (1970), Blaxter and Ehrlich (1974), etc.). Examples of PNR are given in Table 3.

In the cases of both herring and plaice, the number of days to PNR increases as the lapse of days after hatching increases. In other words, the ability of older larvae to endure starvation is stronger than that of younger larvae. Thus, the ability to endure starvation, which depends on the quantity of yolk, may be a primary factor in larval survival.

Table 3. Days to point-of-no-return (PNR) (After Blaxter and Ehrlich, 1974)

| Species | Age, days from <br> hatching of stage | Days to <br> PNR |
| :--- | :--- | :---: |
| Herring | 6 end of yolk sac stage | 6 |
|  | 30 | 8 |
| Plaice | 50 | 8 |
|  | 74 | 12 |
|  | 88 | 15 |
|  | End yolk sac stage | 6 |
|  | Stage $3^{\text {a }}$ | 15 |

${ }^{\text {a }}$ See Ryland (1966)

Hatching periods of marine fish eggs differ according to the species but, generally speaking, the eggs of the low temperature inhabiting species tend to have a longer hatching time than those of the high temperature inhabiting species (Table 2). This may be due to the difference in temperature of the water which each species inhabits.

The critical period of high mortality at the young stages normally occurs immediately after hatching. Therefore, it is of utmost importance to observe and trace the fluctuating trends of stocks at the stage just after hatching.

### 2.1.2 Critical period of larval survival

The hypothesis of a "critical period (of high nortality rate)" was set up by Hjort (1914). Hjort established that the year-class strength of the Norwegian herring and cod stocks varied widely and that the strength of a year-class was determined early in its history. He went on to say, "This \{------\} leads us to the question, at which stage of development the most critical period is to be sought. Nothing is known with certainty as to this; such data as are avilable, however, appear to indicate the very earliest larval and young fry stages as most important (Hjort, 1914, p. 204; original emphasis)".

The population fluctuation of fishes comes about in a shifting stage from one generation to the next; that is to say in a reproduction stage, and continues in approximately the same relation to that of other year classes throughout the life of the individuals. This phenomenon was confirmed for several fish species such as herring, horse mackerel, sardine etc.. The fluctuation of stocks in a reproduction stage would be decided by the mortality rate during the early life history as Hjort pointed out. Therefore, only 1 percent or less fluctuations of survival rate in the early life stage would bring widely different fluctuations of stocks of recruitment.

The first work which deals critically with the early survival rate of marine fish is that of Sette (1943) on Atlantic mackerel (Scomber scombrus) of North America. Figure 4 suggests that the critical period (a period of high mortality) of Atlantic mackerel may be characterized at age 40 days, or larval length of $9-10 \mathrm{~mm}$, and this period coincides with the ensuing period during the transition from larval to post-larval stages.


Figure 4. Survival of young stages of Atlantic mackerel.
(From Sette, 1943, Figure 17.)
As regards sardine (Sardenops melanosticta) of Japanese coastal waters, Nakai \& Hattori (1962) estimated the survival curve during the early life history by using the specimens from plankton net sampling.

Figure 5 reveals that the number of individuals decreases abruptly during the 2-week period after spawning; especially catastrophic mortality is shown at five days after spawning (this period coincides with the transition from hatch to pre-larval stages).


Fig. 5 Survival of sardines at early stages estimated from vertical collection 1949-5l.
(After Nakai \& Hattori, 1962)

Both cases cited above seem to provide evidence of the critical period in the early life history. However, this sharp drop in the estimated survival curves may arise from one of the three causes; (1) it may actually represent a period of high mortality, (2) it may represent a period when the larvae are not caught in proportion to their true abundance (Fig. 6) (either because of increased swimming and net-dodging ability or because some of them have moved out, horizontally or vertically, of the water sampled by the nets), or (3) it may represent a temporary period of reduced rate of growth.

So the question concerning the existence of a critical period in the early life history of marine fishes cannot yet be answered categorically. Thus, although the field data show weak points which make stock assessment difficult, the field approach gives rise to questions which enable experimental research to be conducted.


FIGURE 6. Analysis of length-frequency data for daylight catches of stolephorus from 44 paired samples. Purse seine data closed circles, a measure of absolute abundance, are approximated by the straight line, $N_{L}$. Catch with the $1-m$ net, $C_{L}$, has been corrected for changes in population $(N)$ with length ( $L$ ) , $C_{L} / N$, which shows the minimum probability of capture, $P$, as a function of length for the $1-m$ ne $£$. Data from Murphy and Clutter (1972). (After Barkley, 1972)

### 2.2 Factors controlling larval survival

### 2.2.1 Food density

Several rearing tests to ascertain whether high larval survival and growth rates are ensured by the supply of a high density of food have been carried out ( $O^{\prime}$ Connell and Raymond (1970), Lasker et al. (1970), Saksena and Houde (1972), Wyatt (1972), Hunter (1972), Hunter and Thomas (1974)). These studies reveal that under experimental conditions, high larval survival and growth rates are maintained at a proper degree of food density. For example, in the case of larval anchovy (Anchoa mitchilli), survival and growth rates increase with the increment of prey density until the prey reach a density of 4 individuals per 1 ml of water (Fig. 7). That is to say, a density of prey of at least $1-2$ individuals/ml is required for the survival of larval anchovy.

Similar work with marine fish larvae was carried out and has indicated that various kinds of fish larvae were successful in securing a proper amount of food during their first short periods of feeding (Table 4).


Fig. 7 Calculated growth rates of Anchoa mitchilli larvae and mean concentration of food organism in the rearing tanks during each experiment. (After Saksena \& Honde 1972)

Table 4. Feeding efficiency of marine fish larvae at the end of the yolk sac stage, and estimates of required food concentrations. (Feeding efficiency $=\%$ successful feeding strikes)

|  | Length at <br> first feeding <br> $(\mathrm{mm})$ | Feeding <br> efficiency <br> $(\%)$ | Required food <br> density <br> $($ no. $/ 1)$ |
| :--- | :--- | :--- | :--- |

$1^{\text {Variation }}$ due to different assumptions about accuracy of predation.
2 variation between experiments.
${ }^{3}$ Variation between larvae.
${ }^{4}$ Depends on food type.
${ }^{5}$ Density of Artemia nauplii required to keep larval digestive tract full.
${ }^{6}$ Density of rotifers required to meet metabolic demand.

However, the values of density calculated under experimental conditions do not correspond to those calculated on the basis of the field survey. This may be owing to under-estimation of prey density in the field, as already pointed out. Both larvae and prey distribute patchily in the field. Therefore, if early larval stage anchovy (even at the yolk sac stage) could find and feed on the patchy prey in the field, they would survive and grow because the available food would be sufficient.

### 2.2.2 Predation

Predation on fish larvae is also a major factor affecting the survival of larvae. The predators comprise small plankton, other fish and adult fish of the same species (cannibalism). Laboratory studies on predation by Copepods or Euphausiid shrimps on fish larvae were carried out by Lillelund and Lasker (1974), Theilacker and Lasker (1974). These studies reveal that plankton such as Copepods and Euphausiid may be important predators of fish larvae. Especially within the adult Euphausiid (Copepods) size group, feeding on fish larvae increased significantly with increasing body size (Fig. 8) and abruptly decreased with the development of the larval fish stage (Fig. 9). As far as predators such as zoo-plankton are concerned, it is estimated that they are abundant at the fish spawning and nursery grounds.

Thus the problem of predation by various enemies must not be ignored.


Fig. 8. Number of anchovy eaten per day by individual larval, juvenile, and adult E. pacifica (open circles). Closed circles indicate the median number of anchovy larvae eaten (with extremes given by the solid lines) when 7 individuals were fed daily for 5 consecutive days
(After G.H. Theilacker and R. Lasker, 1974)


Fig. 9. The effect of the age of the anchovy larva and the addition of an extra prey (Artemia naup lii) $^{\prime}$ on larval mortality due to predation by Labidocera trispinosa females. (After Lillelund \& Lasker, 1971)
3. NEED FOR COMBINED SURVEY (FIELD AND REARING)

As indicated above, the research on early life history of marine fish population can be conducted either by means of field surveys or rearing studies. If experimental research by rearing were carried out in isolation, it would be far removed from natural conditions. Therefore, a two-pronged approach (field and rearing experimental surveys) have a considerable contribution to make to studies on eggs, larvae and early life history with emphasis on stock assessment of marine fish.

As regards tropical fish species, the introduction of rearing techniques present both advantages and disadvantages. On the one hand, samples of eggs and larvae can easily be obtained from the field at any time, because tropical fish species generally have a long spawning period and a short life span. On the other hand, tropical fish have a low threshold to environmental factors such as temperature, salinity, etc., that is they are highly sensitive to change in environmental conditions.

Further progress in setting up rearing techniques can be achieved only if the above problems are taken into consideration.

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